

## New findings and an overview of the oligochaetous Clitellata (Annelida) of the North Atlantic deep sea

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*Abstract.*—Six species of Tubificidae are reported from abyssal depths (over 2600 m) off New York/New Jersey in the Northwest Atlantic Ocean. Two members of the subfamily Phallo-drilinae, *Bathydrilus medius* Erséus, 1983 and *B. sandersi* Erséus, 1983, previously known only from deep-sea localities in the Northeast Atlantic, are described. The known depth distributions of all deep-sea oligochaetes known to occur in the North Atlantic (38 species of Tubificidae, three species of Enchytraeidae) are analysed, and their pattern suggests that, while abyssal species tend to be distributed on both sides of the ocean, the bathyal taxa are largely endemic to either the American or the European continental slopes.

In the course of a study of rates and magnitude of trace metal redistributions following the end of sludge dumping at the 106-Mile Dumpsite on the continental rise off New York/New Jersey (Dr. J. Frederick Grassle, Principal Investigator), new material of deep-sea clitellates (families Enchytraeidae and Tubificidae) was collected and placed at our disposal.

The tubificids from this collection are reported in the present paper. Two of them, *Bathydrilus medius* Erséus, 1983a and *B. sandersi* Erséus, 1983a, were first described from similar depths off Ireland in the Northeast Atlantic (Erséus 1983a), and the new records are thus a considerable range extension. As there is limited access to collections of oligochaetous Clitellata from the deep sea, the new American specimens of these two species are described in this paper. One new deep-sea species of enchytraeid, *Grania papillinasus*, found during the dumpsite study as well as on the European side of the North Atlantic, was recently described by Rota & Erséus (2003). The distributional pattern of all known

North Atlantic deep-sea oligochaetes is analyzed herein.

### Material and Methods

The worms studied originate from nine dives with the submersible “*Alvin*,” undertaken in June 1996 during the “Atlantic II” cruise #133 at the 106-Mile Dumpsite area off New York/New Jersey. The actual dumpsite (38.8°N, 72.1°W) is located about 106 miles SE off New York City, i.e., east of the mouth of Delaware Bay, where dumping of sewage sludge was done between 1989 and 1992. All dives were made to similar depths but at various distances from the dumpsite, including two reference dives at about 39.3°N, 70.7°W (S of Massachusetts) (J. Frederick Grassle, personal information).

The specimens were fixed in formalin, stained with Rose Bengal, and stored in 70% ethanol. They were later stained with alcoholic paracarmine and mounted whole in Canada balsam. The measurements in the descriptions refer to this whole-mounted

material, examined by a light microscope. The material is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., and the Swedish Museum of Natural History (SMNH), Stockholm.

### Taxonomy

Class Clitellata

Family Tubificidae

Subfamily Phallodrilinae

Genus *Bathydrilus* Cook, 1970

*Bathydrilus medius* Erséus, 1983

Fig. 1A–B

*Bathydrilus medius* Erséus, 1983a:140–142, fig. 9.

*New material examined.*—USNM (1018636), sexually mature specimen in two parts (on two slides), from continental slope S of Massachusetts, U.S.A., 39.33°N, 70.66°W, 2610 m (*Alvin* dive # 3076); 8 Jun 1996. USNM (1018637), immature specimen in two parts (on two slides), from same dive.

*Description of new, sexually mature specimen.*—Length 6.4 mm, 37 segments. Width at clitellum 0.33 mm, but this region much flattened by coverslip; preclitellar and postclitellar parts of body only 0.08–0.14 mm wide. Prostomium damaged. Clitellum well developed, extending over 1/2X–XII. Chaetae (Fig. 1A) bifid, with diverging, subequal teeth; upper tooth slightly thinner than lower. Bifids 55–65  $\mu\text{m}$  long, 2–2.5  $\mu\text{m}$  thick, three to four per bundle in preclitellar segments, two per bundle in mid-body, mostly three per bundle in posterior part of body. Ventral chaetae of segment XI absent. Male pores paired, in line with ventral chaetae, in middle of XI; each pore as a small copulatory sac covered by a papilla formed by a fold of body wall. Spermathecal pores paired, in anteriormost part of X; pores appear dorso-lateral, but exact position not established.

Pharyngeal glands poorly developed. Male genitalia (Fig. 1B) paired. Vas defer-

ens about 7  $\mu\text{m}$  wide, thin-walled, not observed in its whole length, but entering ectal part of atrium. Atrium cylindrical, sigmoid, totally about 270  $\mu\text{m}$  long, with entalmost part about 50  $\mu\text{m}$  wide, tapering to about 25  $\mu\text{m}$  wide at ectal, duct-like part. Most of atrium heavily muscular, with muscle layer up to about 7  $\mu\text{m}$  thick; ectal duct less muscular. Atrium opening into small copulatory sac. Ental, apical end of atrium in posterior end of segment XI. Anterior prostate gland communicating with ectal part of atrium, near entrance of vas deferens. Posterior prostate located near ental, apical end of atrium, and extending into XII, but actual entrance into atrium not observed. Spermathecae elongated oval, about 135  $\mu\text{m}$  long, about 70  $\mu\text{m}$  wide, but exact outline not clear in specimen; ducts inconspicuous, ampullae with large globules of secretion (in walls?) and irregular lumen containing loose sperm.

*Remarks.*—The second specimen is immature, but its somatic features conform to those of the sexually mature worm.

*Bathydrilus medius* was originally described on the basis of two specimens from a locality at about 3350 m depth, southwest of Ireland (Erséus 1983a). The present mature specimen has more sigmoid atria than those reported for the type material, but this may be merely a result of muscular contraction (i.e., shortening) of its body. More noteworthy is that its spermathecal pores appear to be dorso-lateral, rather than lateral as was clearly observed for the Northeast Atlantic material (Erséus 1983a:141); we did not find it necessary to re-examine the type specimens. However, even if this difference is real (i.e., if the present worm indeed has dorso-lateral pores), it could be interpreted as intra-specific, considering the great geographical distance between the two populations of *B. medius* studied.

*Distribution and habitat.*—South of Massachusetts (U.S.A.) in Northwest Atlantic (new record), and off Ireland/France in Northeast Atlantic. Deep-sea sediment, 2610–3356 m depth.

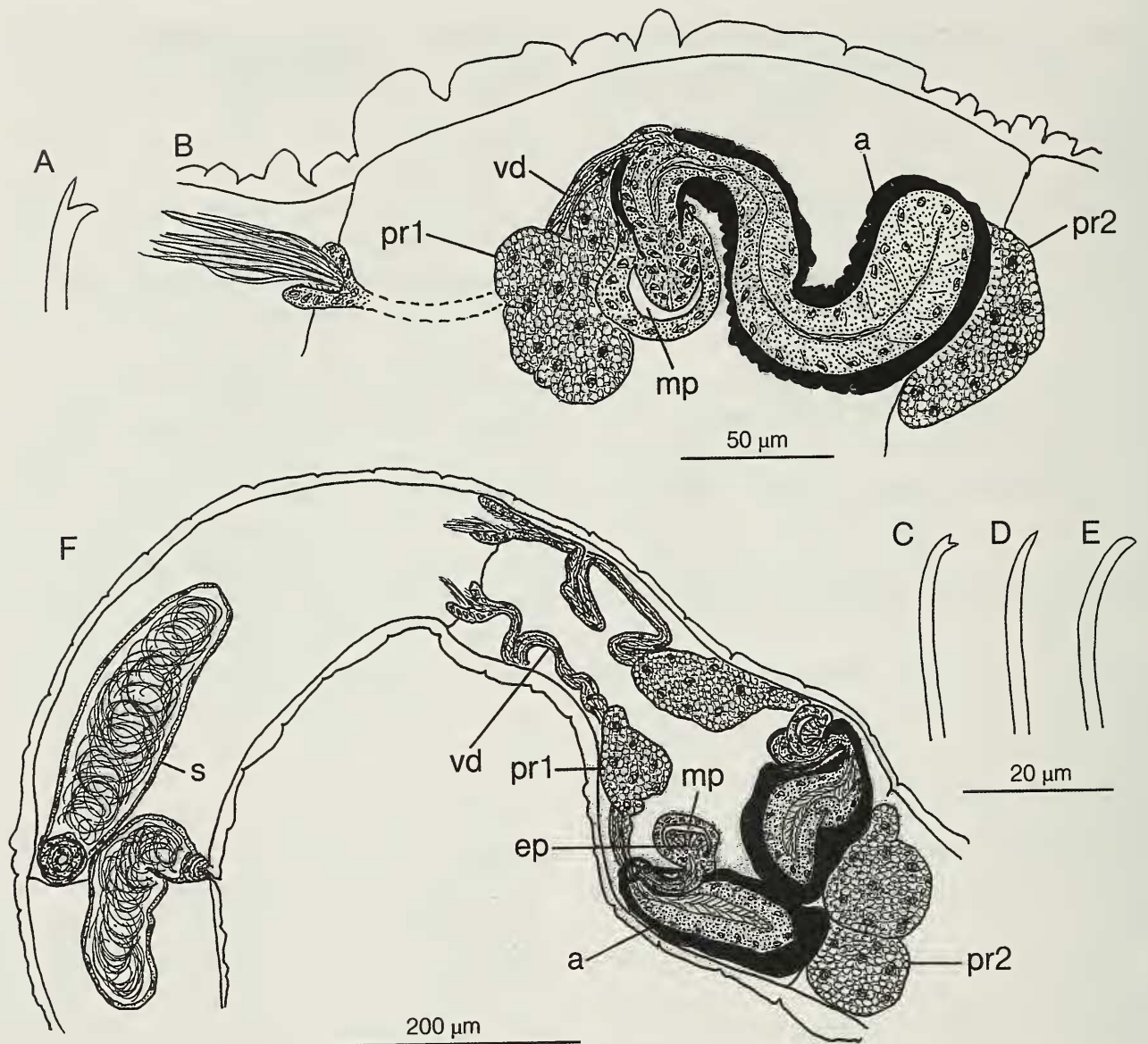


Fig. 1. A, B: *Bathydriilus medius* Erséus. A, Free-hand drawing of chaeta (ectal portion). B, Ventral view of male genitalia in segment XI. C–F: *Bathydriilus sandersi* Erséus. C, Ectal portion of chaeta from segment III. D, Ectal portion of chaeta from segment IV. E, Ectal portion of chaeta from posterior end of worm. F, Ventral view of male genitalia and spermathecae in segments X–XI. Abbreviations: a, atrium; ep, epidermal papilla; mp, male pore; pr1, anterior prostate gland; pr2, posterior prostate gland; s, spermatheca; vd, vas deferens.

*Bathydriilus sandersi* Erséus, 1983

Fig. 1C–F

*Bathydriilus sandersi* Erséus, 1983a:139–140, fig. 8.

*New material.*—USNM (1018638–1018639), two specimens (one complete, sexually mature; the other a posterior end only) from continental slope E of Delaware, U.S.A., 38.57°N, 72.50°W, 2625 m (*Alvin* dive # 3078); 10 Jun 1996. SMNH Main Coll. 46160–46161, two sexually mature specimens from same site, but 2630 m (dive # 3077); 9 Jun 1996.

*Description.*—Length of single complete specimen 10.5 mm, with 43 segments. Width at segment XI, 0.19–0.24 mm. Pro-stomium pointed, triangular, rather muscular, and with more or less demarcated apical papilla. Anus somewhat subterminal on pygidium. Clitellum poorly developed. In segments II–III, chaetae bifid with upper tooth slightly smaller than lower (Fig. 1C) or single-pointed (Fig. 1D); these chaetae about 50  $\mu$ m long, about 2  $\mu$ m thick, generally one or two (occasionally three or zero) per bundle. From IV onwards, chaetae sharply single-pointed (Fig. 1E), 55–70  $\mu$ m long,

2–3  $\mu\text{m}$  thick, two to four (occasionally one) per bundle; those of postclitellar segments seldom more than two per bundle. Chaetae absent from segment bearing male pores; no modified genital chaetae present. Male pores paired, in line with ventral chaetae, located posterior to middle of segment X (one specimen) or XI (two specimens). Spermathecal pores paired, located dorsal to lateral lines, almost in line with dorsal chaetae, in anteriormost part of segment immediately preceding the male pore segment.

Pharynx wide, conspicuous. Pharyngeal glands poorly developed. Male genitalia (Fig. 1F) paired. Vas deferens about 10–13  $\mu\text{m}$  wide, thin-walled, somewhat coiled, entering (together with stalk of anterior prostate gland) ectal end of atrial ampulla; i.e., approximately where atrium narrows abruptly to form its ectal duct (see below). Atrium consisting of oval-to-spindle-shaped (generally somewhat twisted) ampulla, 135–160  $\mu\text{m}$  long, 60–100  $\mu\text{m}$  wide, with 10–20  $\mu\text{m}$  thick muscular layer and somewhat granulated and ciliated inner epithelium, and ectal muscular duct; latter shorter and distinctly narrower than ampulla and leading to copulatory organ. This organ an epidermal papilla (Fig. 1F, ep) inside a small copulatory sac. Spermathecae (Fig. 1F, s) consisting of narrow, short, but distinctly muscularized ducts, and thin-walled, oblong ampullae; latter 160–240  $\mu\text{m}$  long, 70–90  $\mu\text{m}$  wide, lacking muscular layer, but containing dense masses of sperm.

*Remarks.*—This species was originally described on the basis of three specimens from abyssal depths SW of Ireland, in the Northeast Atlantic (Erséus 1983a). The new material conforms well to the original description, even in terms of dimensions of the chaetae and various genital structures. It is particularly noteworthy that the genitalia are located in segments IX–X in one of the new specimens from the Northwest Atlantic, while genitalia normally are in X–XI in tubificids; the genitalia were in such a forward position (in either VIII–IX, or

IX–X) also in the three Northeast Atlantic specimens.

The presence of an epidermal papilla inside each copulatory sac was noted as a possibility in the original description (Erséus 1983a:140: “..atrial duct opening into a deep vagination, the wall of which is thickened at inner end (possibly a papilla is present here, as in *B. meridianus* Erséus (1979a, fig. 6); but this is not quite clear in available material)”); see also Erséus (1983a, fig. 8C), where the thickening is depicted, albeit partly hidden by the atrial duct). The papillar nature of the structure is confirmed by the new material of *B. sandersi* (Fig. 1F, ep).

This study has also shown that *Bathydriilus sandersi* has a somewhat muscular prostomium equipped with a small apical papilla, a feature shared by three other deep-sea species of *Bathydriilus*, *B. asymmetricus* Cook, 1970a, *B. atlanticus* Erséus, 1979a, and *B. hadalis* Erséus, 1979a. It is noteworthy that two deep-sea representatives of the large genus *Grania* Southern, 1913 (family Enchytraeidae), *G. torosa* Rota & Erséus, 2003, and *G. papillinasus* Rota & Erséus, 2003, possess similar frontal papillae (see Rota & Erséus, 2003, figs. 12A, 13A). Other deep-sea Tubificidae (e.g., *Atlantidrilus hamulus* Erséus, 1992, *Mexidrilus grasslei* (Erséus, 1984), and *M. obtusus* Erséus, 1992) have triangular prostomia but with less demarcated tips, while at least two abyssal species, *Atlantidrilus rostratus* (Erséus, 1984), and *Adelodrilus fimbriatus* Erséus, 1983b, appear even further modified; their prostomium as a whole being prolonged into a conspicuous muscular “snout.”

The occurrence of muscle fibers in the prostomium is reported for members of several oligochaetous families. Such musculature, which is embryologically derived from a forward extension of the anterior ends of the mesodermal bands (Dales 1963, Anderson 1973), takes either the form of parietal layers (the circular and longitudinal ones sometimes arranged in a reversed or-

der with respect to that characteristic of the segmental body wall, e.g., in the haplotaxid *Haplotaxis ichthyophagous* Gates, 1971, Brinkhurst & McKey-Fender 1991), or of muscle strands or laminae running transversely across the lumen of the prostomium (e.g., in species of the enchytraeid genera *Achaeta* and *Oconnorella* (Vejdovsky, 1884: plate VII, fig. 1, Rota & Healy 1999), or, particularly for species with elongate prostomia, of longitudinal straps running backwards to the walls of the first two segments (e.g., in the "criodrilid" *Criodrilus lacuum* Hoffmeister, 1845 [family Almidae according to Jamieson, 1988]; Vejdovsky, 1884: plate XIV, fig. 1). By contraction of the circular parietal musculature or of transverse luminal fibers, the prostomium narrows, whereas contraction of the longitudinal fibers produces its shortening or even its retraction into the peristomium (both changes of shape are reported in the Tubificidae, e.g., in species of *Duridrilus*, *Limnodriloides*, and *Tectidrilus*; see Erséus 1990a, b). Such a deformable cephalic end can be used in combination with the buccal lips for food manipulation (e.g., in megadriles; Darwin 1881, Gates 1982) or as a sensitive proboscis for exploring the surroundings [as hypothesized for *Capilloventer longicapitus* Pinder & Brinkhurst, 1997 (*Capilloventridae*); see original description]. However, for animals dwelling in fine deep-sea sediment, heavily muscularized, movable prostomia are likely to be primarily an adaptation for burrowing, in contrast to the situation for the interstitial oligochaetous species commonly inhabiting sandy continental shelf bottoms. Until more detailed morphological studies have been made, the function of the apical papilla remains unclear, but we propose it may act as a sensory structure. At any rate, as such papillae are rare among other marine tubificid taxa, as well as among the many shallow-water *Grania* species, we can assume their independent evolution (by convergence) in at least two lineages of deep-sea oligochaetes.

*Distribution and habitat.*—E of Dela-

ware (U.S.A.) in Northwest Atlantic (new record), and SW of Ireland in Northeast Atlantic. Deep-sea sediment, 2625–3356 m depth.

#### Other Tubificidae

The following species (all except *T. aculeatus* are members of Phallodrilinae) were also found in this study (see Table 1 for authorities).

*Tubificoides aculeatus* (Tubificinae) was collected during all dives (including those at the dump site, E of Delaware), at 2603–2630 m. This species is already well known from many stations, at 1330–2946 m, S of Massachusetts (Cook 1970a, b; Erséus 1984).

*Mexidrilus grasslei* and *Adelodrilus fimbriatus* were found at eight and four dive sites (including some at the dump site, E of Delaware), respectively, in both cases ranging 2603–2630 m. Both taxa were previously known from the continental slope S of Massachusetts, at about 1800 m (Erséus 1983b, 1984). *Mexidrilus grasslei* also occurs at 1330 m depth in the Gulf of Mexico (Erséus 1988).

Finally, a single specimen of *Atlantidrilus biparis* was encountered during dive # 3078 (E of Delaware, 2625 m). This species is already known from S of Massachusetts (at 1764 m; Erséus 1984), as well as from W of Brittany, France (at 2160–2798 m; Erséus 1983a).

#### Discussion

*Bathydrilus medius* and *B. sandersi* are new records for the Northwest Atlantic Ocean, whereas the other tubificids found in the present study were already known from this sector of the continental slope/rise off the eastern U.S.A.

Deep-sea oligochaetes were first described by Cook (1970a, b), and have subsequently been reported from all major oceans. This paper deals with the North Atlantic species, but tubificids have been obtained from great depths also in the Indian

Table 1.—Oligochaete species exclusively reported from depths greater than 200 m in the North Atlantic Ocean, ordered according to their deepest known record; data compiled from Coates & Erséus (1985), Cook (1970a, b), Erséus (1979a, b, 1982a, b, 1983a, b, 1984, 1988, 1989c, d, 1991, 1992), Erséus & Milligan (1989), and Rota & Erséus (2003). All except *Grania* spp. (Enchytraeidae) are members of Tubificidae. Species distributions are indicated for the western (“West”, Northwest Atlantic) and eastern (“East”, Northeast Atlantic) sides of the ocean.

Species	Distribution		Depth range (m)
	West	East	
<i>Tubificoides</i> sp. ?*	X	—	2000–4850
<i>Bathydrilus atlanticus</i> Erséus, 1979a	X	X	1600–4632
<i>Abyssidrilus remus</i> (Erséus, 1979b)	X	—	2900–3753
<i>Abyssidrilus profundus</i> (Cook, 1970a)	X	X	1800–3753
<i>Atlantidrilus rostratus</i> (Erséus, 1984)	X	—	3670–3685
<i>Adelodrilus fimbriatus</i> Erséus, 1983b	X	—	1839–3685
<i>Atlantidrilus quadrisetis</i> Erséus, 1982a	—	X	3338–3356
<i>Bathydrilus sandersi</i> Erséus, 1983a	X	X	2625–3356
<i>Bathydrilus medius</i> Erséus, 1983a	X	X	2610–3356
<i>Abyssidrilus potens</i> Erséus, 1992	X	—	3006–3011
<i>Abyssidrilus opulentus</i> Erséus, 1992	X	—	2002–3009
<i>Tubificoides aculeatus</i> (Cook, 1970b)	X	—	1330–2946
<i>Bathydrilus commexus</i> Erséus, 1988	X	—	618–2902
<i>Grania papillinasus</i> Rota & Erséus, 2003	X	X	2630–2885
<i>Atlantidrilus styloatriatus</i> (Erséus, 1979b)	—	X	2875
<i>Bathydrilus longiatriatus</i> Erséus, 1983a	X	—	622–2853
<i>Bathydrilus desbruyeresi</i> Erséus, 1983a	—	X	2730–2825
<i>Atlantidrilus vulnus</i> (Erséus, 1983a)	—	X	2205–2798
<i>Atlantidrilus biparis</i> (Erséus, 1983a)	X	X	1764–2798
<i>Mexidrilus grasslei</i> (Erséus, 1984)	X	—	1330–2630
<i>Gianius cristolatus</i> (Erséus, 1983a)	—	X	2160–2227
<i>Pirodrilus pinguis</i> (Erséus, 1983a)	—	X	2165–2207
<i>Atlantidrilus hamulus</i> Erséus, 1992	X	—	2114
<i>Bathydrilus asymmetricus</i> Cook, 1970a	X	—	1330–2064
<i>Adelodrilus voraginus</i> (Cook, 1970a)	X	—	1839–2000
<i>Abyssidrilus altoides</i> Erséus, 1992	X	—	1991
<i>Bathydrilus graciliatriatus</i> Erséus, 1979a	—	X	1491–1800
<i>Grania torosa</i> Rota & Erséus, 2003	—	X	1170–1800
<i>Grania atlantica</i> Coates & Erséus, 1985	X	X	556–1796
<i>Phalodriloides lobatus</i> (Erséus, 1983)	X	—	1456–1518
<i>Limnodriloides sphaerothecus</i> Erséus, 1982b	X	—	1000–1518
<i>Mexidrilus constrictus</i> (Erséus, 1988)	X	—	625–860
<i>Mexidrilus vescus</i> (Erséus, 1989c)	X	—	840–841
<i>Phalodriloides pinnulatus</i> Erséus, 1992	X	—	807
<i>Mexidrilus obtusus</i> Erséus, 1992	X	—	799
<i>Olavius rallus</i> Erséus, 1991	X	—	583
<i>Tubificoides paracrinitus</i> E. & Milligan, 1989	X	—	540–582
<i>Tubificoides crinitus</i> Erséus, 1989d	X	—	320–547
<i>Tubificoides pequegnatae</i> E. & Milligan, 1989	X	—	540
<i>Limnodriloides olearius</i> E. & Milligan, 1989	X	—	540
<i>Tubificoides bruneli</i> Erséus, 1989d	X	—	242

\* This taxon, identified as “?Peloscoles gabriellae Marcus, 1950” by Cook (1970a), is probably one (or two?) deep-water species of *Tubificoides*, and not identical to *Tectidrilus gabriellae* (Marcus, 1950) (see Erséus, 1982b).

(Erséus 1986) and Pacific Oceans (Erséus 1979a, 1989a, b). The deepest finds so far concern two Pacific phalloporines living in the hadal zone, *Bathydrilus hadalis* at 7298 m in the Aleutian Trench (Erséus 1979a), and *Abyssidrilus hessleri* (Erséus, 1989b) at 5916 m near the Philippine Trench.

Table 1 lists all (41) oligochaete taxa reported exclusively from depths greater than 200 m in the North Atlantic, the deepest record being from 4850 m. Thirty-three species are known from the American side of the ocean, and this includes some records from the Gulf of Mexico, and from off Surinam (north of South America), while a total of 15 species have been found in the deep sea off Europe. Seven species are reported from both sides of the ocean. Although this latter group makes up only about 17% of the total North Atlantic deep-sea oligochaete fauna known to date, a striking pattern with regard to the depth distribution emerges. Five tubificids and one enchytraeid among these seven amphiatlantic oligochaete taxa all extend well into the abyssal zone; i.e., they reach bottoms that are at least between 2798 and 4632 m deep, and none of them has been found shallower than 1600 m. On the other hand, among 21 species solely recorded from bottoms between 242 and 2798 m, only *G. atlantica* (Enchytraeidae) has so far been collected from both sides of the ocean. In fact, *G. atlantica* is known also from the South Atlantic Ocean (Coates & Erséus 1985). Thus, the abyssal oligochaete species, here referring to the species extending their ranges from the continental slope down towards the abyssal plain, tend to be more widely distributed in the North Atlantic than the bathyal species (i.e., those restricted to the continental slopes), which appear to be largely endemic to one or the other side of the ocean. This pattern may be explained by the more or less continuous extension of abyssal habitats across the Atlantic; i.e., although the North American Basin (in the west) is separated from the Canary and North Eastern Atlantic Basins (in the

east) by the Mid-Atlantic Ridge, the latter has numerous passages that are between 3000 and 4000 m deep (see, e.g., The Times' Atlas of the World. Comprehensive ed.).

As reviewed by Wilson & Hessler (1987), there are numerous examples in the literature of deep-sea species that are said to be widespread or even cosmopolitan, but it has also been pointed out (Wilson & Hessler 1987:187) that "the perceived size of species distributions may be directly correlated with the broadness of species concepts." For the North Atlantic deep-sea oligochaetes (Table 1), however, too much lumping does not seem to be a major problem, as such a large majority (83%) of the species are so far recorded only from one side of the ocean.

Due to the scarcity of records, it would be premature to draw any detailed conclusions about the amount of endemism of oligochaetous Clitellata within different parts of the North Atlantic deep sea. The data available suggest that the abyssal species are more widely distributed than the bathyal ones, but this pattern needs to be corroborated (or refuted) by additional collections from various areas of the North Atlantic Ocean. In this context, material from the Newfoundland Basin, the Mid-Atlantic Ridge, and the continental slopes south of Greenland and off the Reykjanes Ridge, all areas from which no oligochaetes are yet recorded, would be particularly important.

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